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Aquatic beetle diversity from Volcán Tacaná, Mexico: altitudinal distribution pattern and biogeographical affinity of the fauna

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Abstract

Results of an aquatic beetle survey at Volcán Tacaná, Mexico, are presented with five altitudinal levels in a monthly sampling regime, aiming to estimate both diversity and altitudinal distribution patterns of the aquatic beetle fauna. The first list of aquatic beetle species from this mountain is presented, comprising 40 species in 32 genera and nine families, with four species recorded for the first time from Mexico and six recorded for the first time from Chiapas. The aquatic beetle fauna is characterized by Elmidae with 20 species, Dytiscidae with eleven species, Dryopidae with three, and Epimetopidae, Hydraenidae, Hydrophilidae, Gyrinidae, Lutrochidae, and Noteridae with one species each. The species composition through the sampled altitudinal gradient (670–1,776 m) was not homogeneous, with the elmid genera *Macrelmis*, *Heterelmis*, *Microcylloepus*, and *Austrolimnius* present at all levels, while *Hexanchorus*, *Neoelmis*, and *Onychelmis* were present at levels 1–3 (673–1,214 m); dytiscids were mostly present at levels 4 and 5 (1,619–1,776 m), and dryopids were present only at levels 1–3. A Parsimony Analysis of Endemicity supports a general partition between altitudinal levels 1–3 and levels 4 + 5.

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Keywords
Aquatic Coleoptera, Central American Nucleus, Chiapas, faunistics, PAE

Introduction

Among the aquatic insects, aquatic beetles (Coleoptera) are one of the largest groups, with ca. 13,000 described species distributed in 30 families in three of the four coleopteran suborders (Short 2017). Within this insect group, the families Dytiscidae and Hydrophilidae are the largest, with ca. 4,300 and 2,900 species, respectively (Szczepański et al. 2018; Nilsson and Hákej 2020). Aquatic beetles are considered to have a great potential for biodiversity and conservation assessment of water habitats, besides their use as water quality indicators (Samir 2017). They have been recorded in all continents, except Antarctica, and inhabit almost all kinds of aquatic habitats from the smallest phytotelmata to large lakes and rivers (Bilton et al. 2019). Their distribution is determined by different ecological factors, including altitude, which plays an important role in aquatic beetle assemblage composition (Pérez-Bilbao et al. 2014).

Previous studies in the Neotropics have found that altitude may have a significant influence on the composition and structure of an aquatic insect community, as some genera may show a wide range of distribution, while others are characteristic of a particular altitudinal level (e.g., Arias 2004; Henriques-Oliveira and Nessimian 2010, in Brazil; González-Córdoba et al. 2015, 2016, 2020; Mosquera-Murillo and Sánchez-Vázquez 2018, in Colombia; Huanachin-Quispe and Huamantico-Araujo 2018, in Peru).

Approximately 583 species of aquatic Coleoptera are known from Mexico (Santiago-Fragoso and Spangler 1995; Arce-Pérez and Roughley 1999), although the actual number is probably greater. Several studies about local aquatic beetle diversity have taken place in Mexico, often aimed to evaluate the ecological condition of riparian systems, yet providing information on a still fragmentary view of this group's biodiversity (e.g., Arce-Pérez and Novelo-Gutiérrez 1990, 1991, 2015; Arce-Pérez 1995; Arce-Pérez and Roughley 1999; Santiago-Fragoso and Sandoval-Manrique 2001; Arce-Pérez et al. 2002; Gómez-Anaya et al. 2004; Navarrete-Heredia and Zaragoza-Caballero 2006; Campbell et al. 2008; Arce-Pérez and Morón 2011; Torres-García and Pérez-Munguía 2013).

The Tacaná volcano, in the southern Mexican state of Chiapas and bordering Guatemala, is a key element of Volcán Tacaná Biosphere Reserve, a protected area relevant for its rich biotic, cultural, and economic value. This reserve is at the northernmost range of the Central American Nucleus or Central American Volcanic Arc and lies within the Mesoamerican Biological Corridor (CONANP 2013), a dynamic biogeographical area resulting from the assembly of biotas of Nearctic and Neotropical origin. Understanding the geographical distribution and the local diversity of aquatic insects is important to assess the patterns and processes of biological diversification (Benzina et al. 2019). This study aims to record the aquatic beetle diversity from Volcán Tacaná as well as to assess their altitudinal distribution patterns and the biogeographic affinities of the fauna to aid our understanding of biological diversification in the region.

Aquatic entomology, taxonomy, biodiversity, and tropical ecosystems might be a few defining keywords in Ralph Holzenthal's philosophy as an academic advisor. These are relevant themes of encouragement for descriptive taxonomy and biodiversity exploration through several years of competing fields of knowledge, such as morphological and molecular approaches to systematics, which in the end are sides of the same disciplinary coin. This contribution is proudly dedicated by ACR, after 25 years of graduation, to Ralph's bright academic career, in the company of young colleagues and AMLL, currently a graduate student and future academic grandchild.

Materials and methods

Study area

The Tacaná volcano, with its summit at 4,092 m asl, is located in southeastern Chiapas state, Mexico, 30 km NE of Tapachula, with its NE half lying in Guatemala. It is part of the Sierra Madre de Chiapas and lies within the Volcán Tacaná Biosphere Reserve, recognized by UNESCO since 2006. This reserve is located in the Chiapas coast hydrological region (RH-23), on the Pacific slope, and includes the basins of the Suchiate, Coatán, Cahoacán, and Cosalapa rivers (CONANP 2013). The reserve exhibits the following climates: humid temperate (higher portions of the volcano at ≥ 2,000 m; mean annual T = 15.3 °C), humid semi-warm (mid portions of the volcano ca. 1,300–2,000 m; mean annual T = 20.7 °C), and humid warm (lower portions of the volcano at ≤ 1,300 m; mean annual T = 24.3 °C), all with abundant summer rains (mean annual rainfall = 4,438.28 mm).

Sampling procedures

Five sampling localities were established, each at an altitude level along the volcano (levels 1–5; Figs 1, 2; Table 1), in order to estimate an altitudinal distribution pattern of species. Besides single sampling sites at each level (locality), levels 3–5 each had a second sampling site (i.e., there was a total of eight sampling sites; Fig. 1, Table 1). Water body and level selection essentially followed availability of lotic systems, as lentic systems are generally missing except for a crater lake at the top of the volcano; absence of permanent streams at higher elevations precluded sampling at uniformly separated levels, particularly between levels 4 and 5.

Level 1. Finca Alianza, municipality of Cacahoatán. The vegetation is evergreen tropical forest. The Cahoacán river (R1) belongs to the Cahoacán basin. The sampling site (15°02.429'N, 92°10.199'W) is located at 673 m asl.

Level 2. Finca Monte Perla, municipality of Unión Juárez. The vegetation is cloud forest. The river Cascada Monte Perla (R1) belongs to the Suchiate basin. The sampling site (15°02.870'N, 92°05.305'W) is located at 998 m asl.

Level 3. Ejido El Águila, municipality of Cacahoatán. The vegetation is cloud forest. On this locality, two rivers were sampled. The first river, La Resbaladilla (R1), belongs to the Cahotán basin, and the sampling site (15°05.564'N, 92°10.849'W) is at 1,214 m asl.

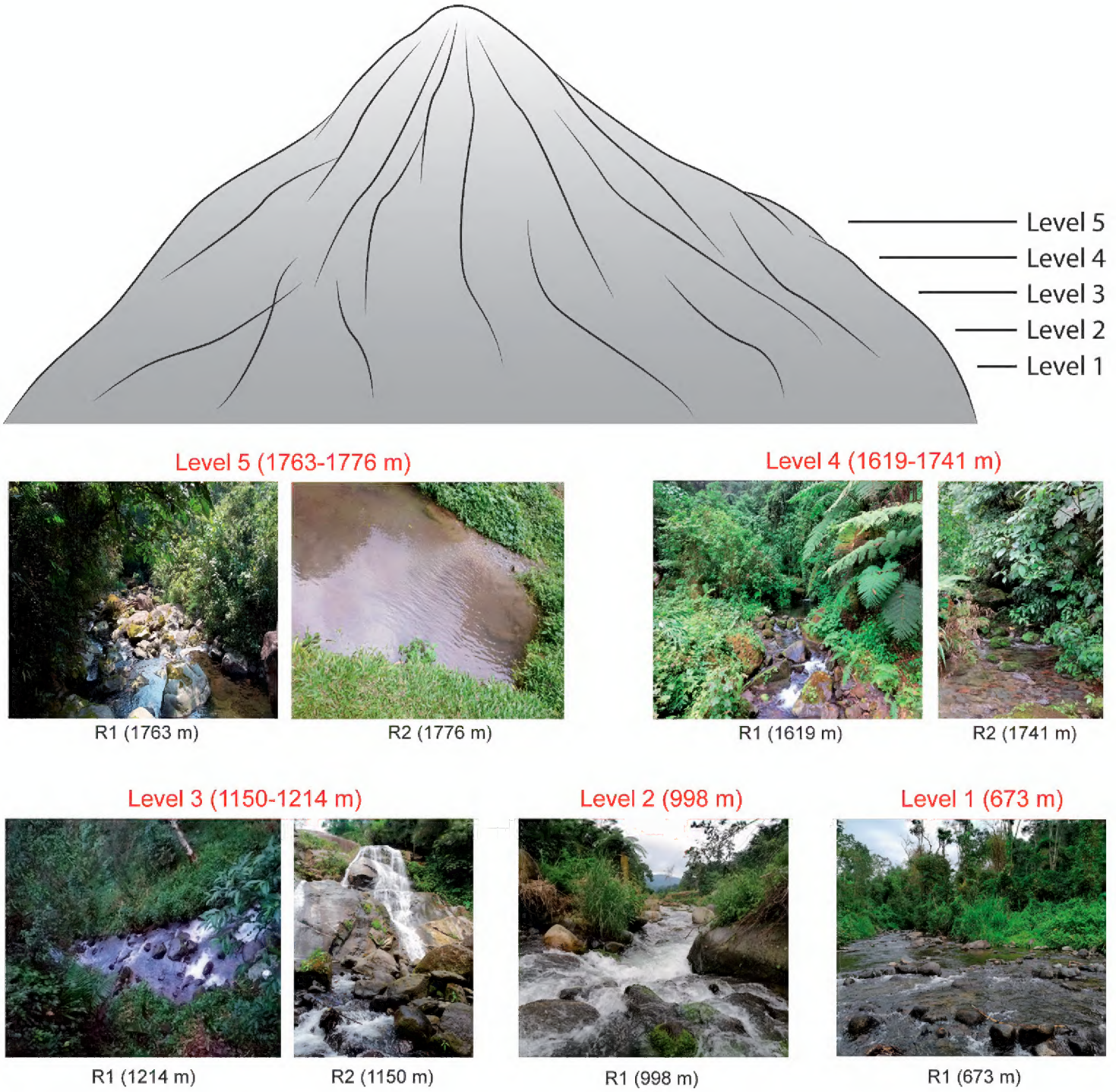

Figure 1. Levels and sampling sites for the aquatic beetle survey along an altitudinal gradient at Volcán Tacaná, Chiapas, Mexico, with habitat examples.

The second river, Cascada La Sirena (R2), belongs to the Coatán basin, and the sampling site (15°06.160'N, 92°11.001'W) is located at 1,150 m asl.

Level 4. Ejido Benito Juárez El Plan, municipality of Cacahoatán. The vegetation is cloud forest. On this locality, two rivers were sampled, both belong to the Cahoacán basin. The first river, El Arroyo (R1), has its sampling site (15°05.946'N, 92°08.540'W) at 1,619 m asl. The second river, La Cascada (R2), has its sampling site (15°05.911'N, 92°08.396'W) at 1,741 m asl.

Level 5. Cantón San Isidro, municipality of Unión Juárez. The vegetation is pine forest. Two rivers were surveyed, both belong to the Suchiate basin. The first river (R1) has its sampling site (15°05.611'N, 92° 05.644'W) at an altitude of 1,763 m asl. The second river (R2) has its sampling site (15°05.588'N, 92°05.537'W) at 1,776 m asl.

The aquatic beetles were sampled monthly over a year (February 2018–February 2019). In each water body (sampling site) three points were selected, separated by 30 m

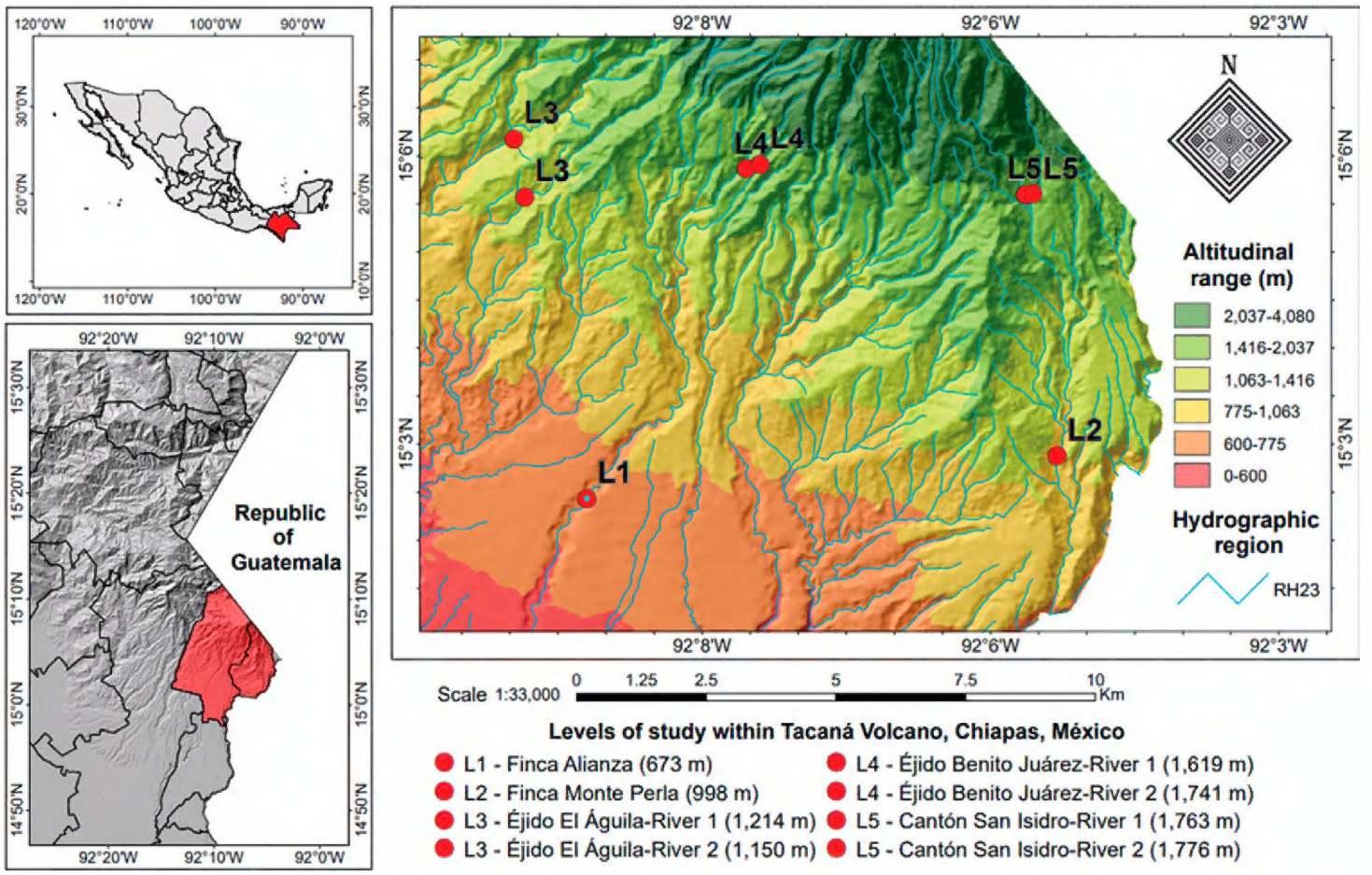

Figure 2. Distribution map of the five sampling levels and for the aquatic beetle survey along an altitudinal gradient at Volcán Tacaná, Chiapas, Mexico.

from each other. Samples were obtained using a D-type benthos net (500 μm mesh), with a dimension of 30.5 cm wide × 53.3 cm long). A second trapping technique, a bucket black-light trap, was used for 3 hours at each sampling site. Captured specimens with organic matter surplus were stored in zippered plastic bags with 80% ethyl alcohol, which was replaced with clean alcohol after 24 hours; aquatic beetles were then sorted from other insect groups in the laboratory using a dissecting microscope, and subsequently identified.

Taxonomic identification

The aquatic beetle specimens were dissected and identified to species using features of the genitalic structures; individual genitalia were extracted and stored in microvials with glycerin. Specimens were mounted on entomological pins, together with their associated labels and genitalia; specimens smaller than 12 mm were placed in paper cartons (points).

Identification was performed through introductory genus-level keys (White and Roughley 2008; Archangelsky et al. 2009; Miller and Bergsten 2016; Benetti et al. 2018; Passos et al. 2018), and subsequently with specialized revisions and original species descriptions.

All the material examined was deposited in the Colección Nacional de Insectos (CNIN) of the Instituto de Biología, Universidad Nacional Autónoma de Mexico.

Parsimony Analysis of Endemicity (PAE)

To aid unravel a general distribution pattern of the aquatic beetle fauna along the altitudinal gradient in the volcano, we performed a Parsimony Analysis of Endemicity (**PAE**).

Table 1. Distribution of aquatic beetle species (Coleoptera) in the sampling levels and sites of Volcán Tacaná, Chiapas, Mexico. 0 = absent; 1 = present. Nea = Neartic; Neo = Neotropical.

FAMILY	SPECIES	SAMPLING POINTS								BIOG. REGIONS
		Lv1	Lv2	Lv3		Lv4		Lv5		
		R1	R1	R1	R2	R1	R2	R1	R2	
Dryopidae	1.*Dryops mexicanus*	1	1	1	1	0	0	0	0	Neo.
	2.*Elmoparnus pandus*	1	0	0	0	0	0	0	0	Neo.
	3.*Helichus suturalis*	1	1	1	1	0	0	0	0	Nea.; Neo.
Dytiscidae	4.*Bidessonotus championi*	0	0	0	0	0	1	0	0	Neo.
	5.*Clarkhydrus* sp.	0	0	0	0	1	1	1	0	Neo
	6.*Copelatus distinctus*	0	0	1	1	1	1	1	1	Nea.; Neo.
	7.*Ilybiosoma flohrianum*	0	0	0	0	0	1	0	1	Neo.
	8.*Laccophilus proximus*	0	0	0	0	1	0	1	0	Nea.; Neo.
	9.*Liodessus affinis*	0	0	0	0	1	0	0	0	Nea.; Neo.
	10.*Neoclypeodytes fryii*	0	0	0	0	1	1	0	0	Nea.; Neo.
	11.*Platambus americanus*	0	0	0	0	1	1	1	1	Neo.
	12.*Rhantus gutticollis*	0	0	0	0	0	0	0	1	Nea.; Neo.
	13.*Thermonectus nigrofasciatus*	0	0	0	0	0	0	0	1	Nea.; Neo.
	14.*Uvarus subornatus*	0	0	0	0	0	1	0	0	Neo.
Elmidae	15.*Austrolimnius formosus*	1	1	1	1	1	1	1	1	Neo.
	16.*Austrolimnius sulcicollis*	1	1	1	1	1	1	1	1	Neo.
	17.*Cylloepus atys*	1	1	1	0	0	1	1	1	Neo.
	18.*Heterelmis glabra*	1	1	1	1	1	1	1	1	Nea.; Neo.
	19.*Heterelmis obesa*	1	1	1	1	1	1	1	1	Nea.; Neo.
	20.*Heterelmis obscura*	1	1	1	1	1	1	1	1	Nea.; Neo.l
	21.*Heterelmis simplex*	1	1	1	0	0	1	1	1	Neo.
	22.*Hexacylloepus metapa*	1	1	1	1	0	1	1	1	Neo.
	23.*Hexanchorus usitatus*	1	1	1	1	0	0	0	0	Neo.
	24.*Huleechius spinipes*	1	1	1	1	0	1	1	1	Nea.; Neo.
	25.*Macrelmis graniger*	1	1	1	1	1	1	1	1	Neo.
	26.*Macrelmis leonilae*	1	1	1	1	1	1	1	1	Neo.
	27.*Macrelmis* sp.	0	0	0	0	0	0	0	1	Neo.
	28.*Microcylloepus inaequalis*	1	1	1	1	1	1	1	1	Neo.
	29.*Microcylloepus troilus*	1	1	1	1	0	1	0	1	Neo.
	30.*Microcylloepus* sp.	1	1	1	1	1	1	1	1	Neo.
	31.*Neoelmis apicalis*	1	1	1	1	0	0	0	0	Nea.; Neo.
	32.*Onychelmis longicollis*	1	1	1	1	0	0	0	0	Neo.
	33.*Phanocerus clavicornis*	1	0	1	1	1	1	0	0	Nea.; Neo.
	34.*Xenelmis bufo*	1	1	1	1	1	1	1	1	Neo.
Epimetopidae	35.*Epimetopus thermarum*	1	0	0	0	0	0	0	0	Nea.; Neo.
Gyrinidae	36.*Gyretes boucardi*	1	0	0	0	0	0	0	0	Neo.
Hydraenidae	37.*Hydraena* sp.	1	1	1	1	1	1	1	1	Neo.
Hydrophilidae	38.*Tropisternus fuscitarsis*	0	1	0	0	0	0	0	0	Nea.; Neo.
Luthrochidae	39.*Lutrochus* sp.	1	0	0	0	0	0	0	0	Neo.
Noteridae	40.*Notomicrus sharpi*	0	0	0	0	0	1	0	0	Nea.; Neo.

According to Morrone (2009) "…PAE constructs cladograms based on the cladistic analysis of presence-absence data matrices of species and supraspecific taxa". A matrix was built with distributional units (i.e., sampling sites) used as "terminals" and species serving as "characters", aiming to obtain a hierarchical structure in the resulting most parsimonious cladograms. Because PAE has been applied to discern a biogeographical signal, such as delimiting areas of endemism or historical relationship between preexisting areas of endemism (Crisci et al. 2003), our assumption is that even a general pattern between altitudinal levels may be informative of a faunistic differentiation along the gradient.

Two analyses were applied: one with the main five levels of sampling (localities) as terminals (i.e., levels 3–5 had sites fused in a single unit), and a second with all eight sampling sites as distribution units or terminals (Table 1). Aquatic beetle species were used as characters, codified as present (1) or absent (0) at each of the distributional units (sampling sites or terminals). A hypothetical distributional unit with all species absent (zero vector) was used to root the trees.

The matrices (Table 1) were built with WinClada (Nixon 2002), then exported as a Nexus file to perform a parsimony analysis in TNT (Tree Analysis using New Technology, version 1.5) (Goloboff and Catalano 2016). The most parsimonious cladogram was obtained through a heuristic algorithm with parameters: random seed = 0, hold = 3000, hold / = 50 in a TBR (tree bisection and reconnection technique) of 60 replicates. The most parsimonious topology was exported to Adobe Illustrator CS5 software to be edited.

Distribution maps

Mapping of the study site with the sampling sites was done with ArcGIS version 10.2. 2. Layers of states and municipalities were obtained from the National Institute of Statistics and Geography (**INEGI**), with information on a 1:50,000 scale. Projection of localities with geographical coordinates was carried out with Universal Transverse Mercator (**UTM**). The raster of the CEM model of the Chiapas area was obtained, a cut of municipalities within the study area was made, with the help of a vector layer of municipal boundaries. The elevation model was adjusted with a reclassification of the z (altitude) values so altitude differences within our area of interest could be visualized. Seven intervals from 0 m to 4080 m were used for the reclassification. In addition, a shadow map (hillshade) was made to better visualize slopes of the terrain of the study area. Finally, layers of the watersheds are located on a scale of 1:50,000, which belongs to the Costa de Chiapas hydrographic region (key RH23).

Results

In total, 23,295 specimens of aquatic beetles of 40 species, distributed in 32 genera and nine families (Dryopidae, Dytiscidae, Elmidae, Epimetopidae, Hydraenidae, Hydrophilidae, Gyrinidae, Lutrochidae, and Noteridae), were collected (Appendix 1). Elmidae had the highest richness with 20 species (50% of total richness). The lowest richness was recorded in Epimetopidae, Hydraenidae, Hydrophilidae, Gyrinidae, Lutrochidae, and Noteridae, with only one species each (2.5% richness, respectively).

We record the following four species from Mexico for the first time (Appendix 1): the Elmidae *Cylloepus atys* Hinton, 1946, *Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020, *Hexanchorus usitatus* Spangler & Santiago-Fragoso, 1992, and the Dytiscidae *Bidessonotus championi* J. Balfour-Browne, 1947. Additionally, four species of Dytiscidae, *Ilybiosoma flohrianum* Sharp, 1887, *Liodessus affinis* Say, 1823, *Neoclypeodytes friyii* Clark, 1862, *Platambus americanus* (Aubé, 1838), one species of

Elmidae, *Huleechius spinipes* (Hinton, 1934), and one of Noteridae, *Notomicrus sharpi* J. Balfour-Browne, 1939, were recorded for the first time from the state of Chiapas.

List of species of aquatic beetles (Coleoptera) from Volcán Tacaná, Mexico

Entries are arranged alphabetically by family and genus. Entries for genera include comments on number of species, and distribution. Species entries include the valid combination, distributional and altitudinal information, as well as type of substrate where they were collected. Altitude or elevation data are given in m above sea level.

Results

Family Dryopidae Billberg, 1820

Genus *Dryops* Olivier, 1791

Dryops mexicanus Sharp, 1882

Note. *Dryops* has a worldwide distribution and comprises 79 species (Shepard and Sites 2016), three of them are recorded from Mexico.

Distribution. Mexico (Chiapas, Morelos), Belize, Costa Rica (Burgos and Trejo-Loyo 2001; Shepard 2004; Barr and Shepard 2017; Zaragoza-Caballero et al. 2019). It has been recorded at an altitudinal range of 200 to 840 m (Barr and Shepard 2017); in this study *D. mexicanus* was collected at levels 1 (670 m), 2 (934 m), and 3 (1,126–1,194 m).

Comments. Collected on substrates consisting of gravel, macrophytes, and leaf packs; found in all sampling months (February 2018 through February 2019, dry and rainy seasons); also collected with a bucket light trap.

Genus *Elmoparnus* Sharp, 1882

Note. This genus includes eight species recorded in the Neotropics (Kodada and Jäch 2005), two of them are recorded in Mexico.

Elmoparnus pandus Spangler & Perkins, 1977

Distribution. Mexico (Chiapas, Oaxaca), Belize, Guatemala, Honduras, Costa Rica, Panama (Spangler and Perkins 1977; Barr and Shepard 2017). The known altitudinal range of this species is 200 to 1,219 m (Spangler and Perkins 1977; Barr and Shepard 2017). In this study, it was collected at level 1 (670 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs (June 2018, rainy season).

Genus *Helichus* Erichson, 1847

Note. This genus is found throughout the Oriental, Nearctic, and Neotropical regions, with 32 species described (Kodada and Jäch 2005).

Helichus suturalis LeConte, 1852

Distribution. United States, Mexico (Chiapas, Durango, Hidalgo), Guatemala, Paraguay (Brown 1972a; Arce-Pérez et al. 2010; Shepard and Aguilar-Julio 2010). The known altitude records of the species are 1,590 and 2,438 m (Brown 1972a; Arce-Pérez et al. 2010). Herein, specimens were found at levels 1 (670 m), 2 (934 m), and 3 (1126–1194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Family Dytiscidae Leach, 1815

Genus *Bidessonotus* Régimbart, 1895

Note. This is one of the largest dytiscid genera in the New World, comprising 36 species (Nilsson and Hájek 2020), with seven species recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Bidessonotus championi J. Balfour-Browne, 1947

Distribution. Mexico (new country record, Chiapas), Guatemala, Honduras, Nicaragua, Costa Rica (Balfour-Browne 1947; Miller 2016; Nilsson and Hájek 2020). The species has been recorded from an altitude of ca. 122 m (Balfour-Browne 1947), herein we recorded the species at level 4 (1,619 m).

Comments. Collected on macrophytes (February 2018, dry season).

Genus *Clarkhydrus* Fery & Ribera, 2018

Note. This genus has a Nearctic and Neotropical distribution and comprises 10 species, seven of which have been recorded in Mexico (Nilsson and Hájek 2020).

Clarkhydrus sp.

Comments. This species was collected at levels 4 (rivers 1 and 2, 1,448–1,619 m) and 5 (river 1, 1,763 m) on substrates of macrophytes and leaf packs, and was present throughout sampling months (February 2018 through February 2019, dry and rainy season). Specimens did not match known described species of the genus; however, they are close to *C. decemsignatus*, yet male genital morphology differs.

Genus *Copelatus* Erichson, 1832

Note. This genus has a cosmopolitan distribution and comprises 454 species (Nilsson and Hájek 2020), 14 of which have been recorded in Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Copelatus distinctus Aubé, 1838

Distribution. United States, Mexico (Baja California, Chiapas, Guanajuato, Jalisco, Morelos, Oaxaca, Puebla, Sonora), Guatemala (Young 1963; Arce-Pérez and Roughley 1999; Zaragoza-Caballero et al. 2019; Nilsson and Hájek 2020). This species has been recorded from moderate elevations (Young 1963) and 1,706 m (Miller and Bergsten 2014), herein it was found at levels 3 (1,126–1,194 m), 4 (1,448–1,619 m), and 5 (1,126–1,776 m).

Comments. Collected on substrates of macrophytes and leaf packs, through all months of sampling (February 2018 through February 2019, dry and rainy season); also collected with a bucket light trap.

Genus *Ilybiosoma* Crotch, 1873

Note. This is a cosmopolitan genus that includes 17 species (Nilsson and Hákej 2020), five of them recorded in Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Ilybiosoma flohrianum (Sharp, 1887)

Distribution. Mexico (Estado de México; Chiapas, new state record; Morelos) (Zaragoza-Caballero et al. 2019; Nilsson and Hájek 2020). There are no published records of altitude for the species; herein, the species was found at levels 4 (1,619 m) and 5 (1,776 m).

Comments. Specimens were found on leaf packs (May 2018, rainy season).

Genus *Laccophilus* Leach, 1815

Note. This cosmopolitan genus is the largest of the subfamily Laccophilinae, with 285 species (Nilsson and Hákej 2020), 26 of which are recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Laccophilus proximus Say, 1823

Distribution. United States, Mexico (Campeche, Chiapas, Coahuila, Oaxaca, San Luis Potosí, Tabasco, Tamaulipas, Yucatán, Veracruz), Belize, Guatemala, Costa Rica, Bahamas, Cuba, Puerto Rico, Guadeloupe (Scheer and Thomaes 2018; Nilsson and Hájek 2020). It has been recorded at altitudes between 14 and 2,438 m (Scheer and Thomaes 2018). In this study, it was collected between 1,126 and 1,723 m.

Comments. Specimens were found on leaf packs (February and March 2018).

Genus *Liodessus* Guignot, 1939

Note. This genus is distributed in North and South America, Africa, and Fiji (Miller and Bergsten 2016) and comprises 40 species (Nilsson and Hájek 2020), with four species recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Liodessus affinis (Say, 1823)

Distribution. Canada, United States, Mexico (Baja California; Estado de México; Chiapas, new state record) (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020). No specific data about altitudinal distribution were found, herein this species was collected at 1,448 m.

Comments. Collected on macrophytes and leaf packs (February and March 2018, dry season).

Genus *Neoclypeodytes* Young, 1967

Note. This genus is present from southwestern Canada south through western United States and Mexico, with a few species in Panama and one in Jamaica (Miller and Bergsten 2016; Nilsson and Hájek 2020). It comprises 27 species (Nilsson and Hájek 2020), 15 of which are present in Mexico (Arce-Pérez and Roughley 1999; Arce-Pérez and Novelo-Gutiérrez 2015; Nilsson and Hájek 2020).

Neoclypeodytes fryii (Clark, 1862)

Distribution. United States, Mexico (Baja California; Chiapas, new state record; Guanajuato; Oaxaca), Guatemala (Miller 2001; Nilsson and Hájek 2020). This species was previously recorded at an altitudinal range between 853 and 1,524 m (Miller 2001). In this study, the species was collected at level 4 (rivers 1 and 2, 1,425–1,619 m).

Comments. Collected on macrophytes and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Genus *Platambus* Thomson, 1859

Note. This genus is distributed in the Nearctic, Neotropical, Palearctic, and Oriental regions, with 67 species (Miller and Bergsten 2016; Nilsson and Hájek 2020), six of which are recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Platambus americanus (Aubé, 1838)

Distribution. Mexico (Chiapas, new state record; Oaxaca), Guatemala, El Salvador (Arce-Pérez and Roughley 1999; Larson et al. 2000; Hendrich et al. 2018; Nilsson and Hájek 2020). Previous altitudinal records are between 1,950 and 2,743 m (Hendrich et al. 2018), while in the present study the species ranged from levels 4 (river 2, 1,619m) to 4 (river 2, 1,776 m).

Comments. Collected on macrophytes and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season); also collected with a bucket light trap.

Genus *Rhantus* Dejean, 1833

Note. This is a cosmopolitan genus with 90 species (Nilsson and Hájek 2020), four of which are recorded in Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Rhantus gutticollis (Say, 1830)

Distribution. Canada, United States, Mexico (Baja California, Coahuila, Colima, Chiapas, Chihuahua, Ciudad de México, Durango, Estado de México, Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo Léon, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Zacatecas), Guatemala, Honduras, Nicaragua, Costa Rica (Blackwelder 1944; Zimmerman and Smith 1975; Balke 1992; Arce-Pérez and Roughley 1999; Larson et al. 2000; Zaragoza-Caballero et al. 2019;

Nilsson and Hájek 2020). This species has been previously recorded from 0 to 2,250 m (Blanco-Aller and Régil 2016), herein it was collected at level 5 (river 2, 1,776 m).

Comments. Collected on leaf packs (May 2018, rainy season).

Genus *Thermonectus* Dejean, 1833

Note. This genus is distributed across the Americas and comprises 20 species and two subspecies (Nilsson and Hajék 2020), with eight species recorded from Mexico (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020).

Thermonectus nigrofasciatus (Aubé, 1838)

Distribution. Mexico (Ciudad de México, Chiapas, Durango, Estado de México, Guanajuato, Hidalgo, Morelos, Oaxaca, Puebla, San Luis Potosí) (Arce-Pérez and Roughley 1999; Zaragoza-Caballero et al. 2019; Nilsson and Hájek 2020). This species was collected at level 5 (river 2, 1,776 m).

Comments. Collected on leaf packs (May 2018, rainy season).

Genus *Uvarus* Guignot, 1939

Note. This genus is distributed worldwide and contains 65 species, nine of which are present in Mexico (Larson et al. 2000; Miller and Bergsten 2016; Nilsson and Hájek 2020).

Uvarus subornatus (Sharp, 1882)

Distribution. Mexico (Chiapas, Oaxaca), Guatemala (Arce-Pérez and Roughley 1999; Nilsson and Hájek 2020). No previous altitudinal records for this species were found. In the present study, this species was found only at level 5 (river 2, 1,776 m).

Comments. Collected on leaf packs (May 2018, rainy season).

Family Elmidae Curtis, 1830

Genus *Austrolimnius* Carter & Zeck, 1929

Note. This genus occurs in the Australasian and Neotropical regions, with more than 100 described species (Manzo 2005, 2007; Jäch et al. 2016). Twenty species of this genus have been recorded in the Americas, from northern Mexico through southeastern Argentina (Hinton 1971; Manzo 2007), with four species recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Austrolimnius formosus (Sharp, 1882)

Distribution. Mexico (Chiapas, Morelos, Guerrero), Belize, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Peru, Brazil, Argentina (Sharp 1882; Hinton 1940b, 1941, 1971; Blackwelder 1944; Shepard 2004; Manzo 2007; Passos et al. 2009; Manzo and Archangelsky 2012; Miranda et al. 2012; González-Córdoba et al. 2016, 2020). Previous altitudinal records of *A. formosus* are from 600 m and 2,438 m (Hinton 1940b). In this study, the species was present in all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Austrolimnius sulcicollis (Sharp, 1882)

Distribution. Mexico (Chiapas, Guerrero), Guatemala, Costa Rica, Panama, Colombia, Venezuela, French Guiana, Ecuador, Peru (Sharp 1882; Hinton 1940b, 1941, 1971; Blackwelder 1944; González-Cordoba et al. 2020). *Austrolimnius sulcicollis* has been previously recorded from altitudes of 600 m and 2,438 m (Hinton 1940b). Herein, this species was collected in all sampling levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling period (February 2018 through February 2019, dry and rainy season).

Genus *Cylloepus* Erichson, 1847

Note. This is the elmid genus with most species in the American continent, with 52 species and 2 subspecies currently known to this region (Segura et al. 2013; Jäch et al. 2016; Silva-Polizei and Barclay 2019), and eight species recorded in Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Cylloepus atys Hinton, 1946

Distribution. Mexico (new country record, Chiapas), Peru (Hinton 1946). Previous altitudinal records are from approximately 500 m (Hinton 1940a). In this study, the species was collected at levels 1 (670 m), 2 (934 m), 3 (river 1, 1,126 m), 4 (river 2, 1,619 m), and 5 (rivers 1 and 2, 1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, through most of the sampling months (except March, July, and September 2018, dry and rainy season).

Genus *Heterelmis* Sharp, 1882

Note. This is a New World genus that comprises 22 species (Silva-Polizei 2018), seven of which are present in Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Heterelmis glabra (Horn, 1870)

Distribution. Mexico (Chiapas, Estado de México, Hidalgo, Jalisco, Morelos, Nayarit, Oaxaca, Tamaulipas, Veracruz), Belize, Nicaragua, Costa Rica (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016). This species was previously recorded from 1,066 m and 1,219 m (Hinton 1940b). Herein, this species was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, through all sampling months (February 2018 through February 2019, dry and rainy season).

Heterelmis obesa Sharp, 1882

Distribution. Mexico (Chiapas, Durango, Estado de México, Hidalgo, Morelos, Oaxaca, Veracruz), Guatemala, Costa Rica, Nicaragua, Peru (Sharp 1882; Hinton 1940b; Blackwelder 1944; Spangler 1966; Brown 1972b; Jäch et al. 2016). This species was previously recorded from 1,463 m and 2,438 m (Hinton 1940b). In this study, the species was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and litter, throughout all sampling months (February 2018 through February 2019, dry and rainy season).

Heterelmis obscura Sharp, 1882

Distribution. Mexico (Chiapas, Colima, Estado de México, Morelos, Nuevo León, Oaxaca, San Luis Potosí, Veracruz), Guatemala, Costa Rica, Colombia, Peru, Brazil (Sharp 1882; Grouvelle 1889; Hinton 1940b; Blackwelder 1944; Brown 1972b; Santiago-Fragoso and Spangler 1995; Passos et al. 2009; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records of *H. obscura* are from 1,463 m and 2,438 m (Hinton 1940b). In this study, the species was found in all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Heterelmis simplex Sharp, 1882

Distribution. Mexico (Chiapas, Morelos), Guatemala, Costa Rica, Peru, Trinidad and Tobago (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al.

2016). No previous altitudinal records were found. This species was collected at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling months (February 2018 through February 2019, dry and rainy season).

Genus *Hexacylloepus* Hinton, 1940b

Note. This genus is distributed in the southwestern United States and the Neotropical region, with 25 described species (Jäch et al. 2016; Silva-Polizei et al. 2020), seven of which are recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016; Silva-Polizei et al. 2020).

Hexacylloepus metapa Silva-Polizei, Barclay & Bispo, 2020

Distribution. Mexico (new country record, Chiapas), Guatemala (Silva-Polizei et al. 2020). There are no previous records of altitude for *H. metapa*, herein the species was collected at levels 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 to February 2019, dry and rainy season).

Genus *Hexanchorus* Sharp, 1882

Note. This is a New World genus and comprises 21 species, with three recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Hexanchorus usitatus Spangler & Santiago-Fragoso, 1992

Distribution. Mexico (new country record, Chiapas), Nicaragua, Costa Rica, Panama.

The known altitudinal record of *H. usitatus* was 1,075 m (Spangler and Santiago-Fragoso 1992). Herein, the species was found from levels 1 (670 m) through 3 (1,126–1,194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season); also collected with a bucket light trap.

Genus *Huleechius* Brown, 1981

Note. This is a North American genus and includes three species (Jäch et al. 2016), with two recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Huleechius spinipes (Hinton, 1934)

Distribution. Mexico (Baja California; Chiapas, new state record; Coahuila; Estado de México; Guerrero; Jalisco; Nuevo León; Oaxaca; Tabasco; Veracruz) (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016). A previous altitudinal record of *H. spinipes* is from 1,524 m (Hinton 1940b). In this study, the species was found at levels 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Genus *Macrelmis* Motschulsky, 1859

Note. This is a Nearctic and Neotropical genus, distributed from southern United States to South America, and comprises 49 species, 10 of which have been recorded from Mexico (Hinton 1940b; Passos et al. 2015; Jäch et al. 2016).

Macrelmis graniger (Sharp, 1882)

Distribution. Mexico (Chiapas, Estado de México, Morelos, Oaxaca), Guatemala, Costa Rica, Nicaragua, Peru (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records of *M. graniger* are from 1,219 and 1,706 m (Hinton 1940b). Herein, this species was collected at level 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Macrelmis leonilae Spangler & Santiago-Fragoso, 1986

Distribution. Mexico (Chiapas, Guerrero, Morelos, Oaxaca, Veracruz), Guatemala, Honduras, Nicaragua, Costa Rica, Peru (Santiago-Fragoso and Spangler 1995; Segura et al. 2013). A previous altitudinal record of *M. leonilae* is 1,075 m (Spangler and Santiago-Fragoso 1986). Herein, this species was collected at level 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (1,763–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Macrelmis sp.

Comments. This species was collected at level 5 (river 2, 1,776 m) on substrates of macrophytes and leaf packs, and was present throughout sampling months (Feb-

ruary 2018 through February 2019, dry and rainy season). Specimens, including males, did not match known described species of the genus, although they are similar to *M. leonilae*. Male parameres of the specimens, in dorsal view, are slightly wider from the base to the apical portion, while in *M. leonilae* they are wider through the basal half.

Genus *Microcylloepus* Hinton, 1935

Note. *Microcylloepus* is widely distributed in the New World and comprises 30 species (Silva-Polizei 2018), five of them recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Microcylloepus inaequalis (Sharp, 1882)

Distribution. Mexico (Chiapas, Estado de Mexico, Morelos, Veracruz), Guatemala, Nicaragua, Costa Rica, Panama, Paraguay, Brazil (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records of *M. inaequalis* are at 1,463 m and 1,525 m (Hinton 1940c). Herein, this species was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Microcylloepus troilus Hinton, 1940

Distribution. Mexico (Chiapas, Estado de Mexico). Previous altitudinal records of *M. troilus* are from 1,707 to 2,286 m (Hinton 1940b). In this study, *M. troilus* was found at all sampled levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season).

Microcylloepus sp.

Comments. This species was collected at levels 1 (670 m), 2 (934 m), 3 (1,126–1,194 m), 4 (river 2, 1,619 m), and 5 (river 2, 1,776 m) on substrates of gravel, macrophytes, and leaf packs, throughout sampling months (February 2018 through February 2019, dry and rainy season). Specimens, including males, did not match exactly known described species of the genus, being close to *M. angustus*. Male genitalia of the specimens have the medium lobe slightly wider than *M. angustus*.

Genus *Neoelmis* Musgrave, 1935

Note. This genus is distributed across the American continent and has 50 described species (Jäch et al. 2016), five of them recorded from Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Neoelmis apicallis (Sharp, 1882)

Distribution. Mexico (Chiapas, Estado de México, Morelos, San Luis Potosí, Tamaulipas), Guatemala, Costa Rica (Santiago-Fragoso and Spangler 1995; Segura et al. 2013; Jäch et al. 2016). Previous altitudinal records were at 137 m and 1,463 m (Hinton 1940b). In this study, the species was found at levels 1 (670 m), 2 (934 m), and 3 (1,126–1,194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, in about half of the sampling period (February to May, and August 2018, and February 2019, dry and rainy season).

Genus *Onychelmis* Hinton, 1941

Note. This genus is distributed in Central and South America, contains eight described species (Linský et al. 2021), and this study provides the northernmost point of its range.

Onychelmis longicollis (Sharp, 1882)

Distribution. Mexico (new country record, Chiapas), Nicaragua, Panama, Colombia (González-Córdoba et al. 2016; Linský et al. 2021). Previous altitudinal records were from 1,219 to 1,828 m (González-Córdoba et al. 2016; Linský et al. 2021). In the present study, the species was found at levels 1 (670 m), 2 (934 m), and 3 (1,126–1,194 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, during three months of the sampling period (February, April, and May 2018, dry and rainy season).

Genus *Phanocerus* Sharp, 1882

Note. This genus is distributed from North America through northern South America, with six described species (Jäch et al. 2016), one recorded in Mexico (Santiago-Fragoso and Spangler 1995; Jäch et al. 2016).

Phanocerus clavicornis Sharp, 1882

Distribution. United States, Mexico (Chiapas, Colima, Guerrero, Hidalgo, Nuevo León, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Veracruz), Belize, Guatemala, Honduras, Costa Rica, Panama, Venezuela, Brazil, Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico (Spangler and Santiago-Fragoso 1992; Segura et al. 2013; Jäch et al. 2016). This species was previously recorded from an altitudinal range of 88–549 m (Hinton 1940b; Spangler and Santiago-Fragoso 1992). Herein, the species was found at levels 1 (670 m), 3 (1,126–1,194), and 4 (1,448–1,619 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs through four months of the sampling period (May, June, July, and August 2018, rainy season); also collected with a bucket light trap.

Genus *Xenelmis* Hinton, 1936

Note. This is a New World, mostly Neotropical genus with 11 described species (Jäch et al. 2016), two of them recorded from Mexico (Santiago-Fragoso and Spangler 1995; Sampaio et al. 2015; Jäch et al. 2016).

Xenelmis bufo (Sharp, 1882)

Distribution. Mexico (Chiapas, Colima, Guerrero, Morelos), Belize, Panama, Venezuela (Segura et al. 2013; Jäch et al. 2016). A previous altitudinal record of *X. bufo* is from 1,219 m (Hinton 1940b). In this study, the species was found at all sampling levels (670–1,776 m).

Comments. Collected on substrates of gravel, macrophytes, and leaf packs, throughout the sampling months (February 2018 through February 2019, dry and rainy season).

Family Epimetopidae Zaitzev, 1908

Genus *Epimetopus* Lacordaire, 1854

Note. This genus is distributed across the Nearctic and Neotropical region, with 56 species described (Perkins 2012), eight of them recorded from Mexico (Arce-Pérez and Morón 2011; Perkins 2012).

Epimetopus thermarum Schwarz & Barber, 1917

Distribution. United States, Mexico (Baja California Sur, Chiapas, Jalisco, Nayarit, Sinaloa, Sonora), Belize, Guatemala, Costa Rica, Panama, Venezuela (Perkins 2012).

This species was previously recorded at an altitudinal range of 5–914 m (Perkins 2012). In this study, the species was found in level 1 (670 m).

Comments. Collected with a bucket light trap (June 2018, rainy season).

Family Gyrinidae Latreille, 1810

Genus *Gyretes* Brullé, 1835

Note. This genus comprises 79 species worldwide (Oygur and Wolfe 1991; Babin and Alarie 2014), seven of them recorded from Mexico (Arce-Pérez and Roughley 1999).

Gyretes boucardi Sharp,1882

Distribution. Mexico (Chiapas, Durango, Tabasco, Veracruz), Costa Rica (Arce-Pérez and Roughley 1999; Blanco-Aller 2014). Previous altitudinal records of *G. boucardi* are from 0–125 m (Blanco-Aller 2014). In this study, the species was found at level 1 (670 m).

Comments. Collected near substrate of macrophytes (October 2018, rainy season).

Family Hydraenidae Mulsant, 1844

Genus *Hydraena* Kugelann, 1794

Note. The genus occurs on all continents except Antarctica and comprises more than 990 species described (Trizzino et al. 2013), 36 of which are recorded from Mexico (Navarrete-Heredia and Quiroz-Rocha 2004).

Hydraena sp.

Comments. This species was collected at all sampled levels (670–1,776 m), on substrates of gravel, macrophytes, and leaf packs, throughout the sampling months (February 2018 through February 2019, dry and rainy season). Specimens were small and fragile, particularly males, and dissection was difficult, moreover genital morphology did not match species in keys, so genus-level identification was considered until further study; females were more abundant in collections.

Family Hydrophilidae Latreille, 1802

Genus *Tropisternus* Solier, 1834

Note. This is a New World genus distributed from northern Canada to southern South America, comprising 60 described species (Hansen 1999; Short and Hebauer 2006; Spangler and Short 2008), 19 of them recorded from Mexico (Arce-Pérez and Morón 2011).

Tropisternus fuscitarsis Sharp, 1882

Distribution. Mexico (Chiapas, Colima, Distrito Federal, Jalisco, Estado de México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Veracruz) (Arce-Pérez and Morón 2011). Previous altitudinal records of *T. fuscitarsis* are from 0–125 m (Blanco-Aller 2014). Herein, the species was found in level 2 (934 m).

Comments. Collected with a bucket light trap (July and August 2018, rainy season).

Family Lutrochidae Kasap & Crowson, 1975

Genus *Lutrochus* Erichson, 1847

Note. This genus comprises 29 species and is distributed across the Nearctic and Neotropical region (Maier and Short 2013, 2014; Maier 2016), with three species recorded from Mexico (Arce-Pérez et al. 2010; Maier 2016).

Lutrochus sp.

Comments. This species was present at level 1 (670 m) and was collected on leaf packs (May 2018, rainy season). Specimens key out to an undescribed genus and species included in Maier (2016), an unpublished doctoral thesis, so a preliminary identification is maintained.

Family Noteridae Thomson, 1860

Genus *Notomicrus* Sharp, 1882

Note. This genus comprises 15 species, 13 of them distributed in the New World (Baca et al. 2014; Guimarães and Ferreira 2019), and two of the latter species recorded from Mexico (Nilsson 2011).

Notomicrus sharpi J. Balfour-Browne, 1939

Distribution. United States, Mexico (Chiapas, new state record; Oaxaca; San Luis Potosí; Tamaulipas), Guatemala, Costa Rica, Panama, Bahamas, Cuba, Jamaica, Dominican Republic, Puerto Rico, Virgin Islands, Guadeloupe (Arce-Pérez and Roughley 1999; Nilsson 2011; Manuel 2015). This species was previously recorded from 0–500 m (Blanco-Aller 2015; Manuel 2015). Herein, the species was found at level 4 (river 2, 1,619 m).

Comments. Collected on substrate of macrophytes (February 2018, dry season).

Altitudinal distribution of the aquatic beetle fauna

The aquatic beetle fauna from Volcán Tacaná is distributed throughout the sampled altitudinal gradient (670–1,776 m), however our initial hypothesis is that species distribution would not be homogeneous. We applied a Parsimony Analysis of Endemism (PAE) as a fast approach to detect a potential faunal partition, with a general finding of the three lower altitudinal levels grouping together (i.e., sharing similar species) and about 40% of the species with a widespread altitudinal distribution. A first PAE (Fig. 3A), including the five levels, each as a single unit, recovered a topology distinguishing two well-defined groups, one composed by the three lower levels (673, 998, and 1,150–1,214 m), and another composed by the two higher levels (1,619–1,741 m and 1,763–1,776 m). A second PAE (Fig. 3B), including each sampled river (i.e., rivers of levels 3–5 considered each as a unit) also recovered a group composed by the three lower levels (levels 1–3), nevertheless two rivers of levels 4 and 5 (i.e., R2 of levels 4 and 5, respectively) were recovered as closer to rivers from levels 1–3 than to other rivers of levels 4 and 5 (i.e., R1 of levels 4 and 5, respectively), yet support for the latter group (levels 1–3 + R2 of L4 and L5) is quite weak. This means that the next well supported group would be all rivers excluding river 1 of level 4.

The most diverse family was Elmidae (see some representatives on Fig. 4), with most species widespread along the five altitudinal levels, with the genera *Austrolimnius* (*A. formosus* and *A. sulcicollis*), *Xenelmis* (*X. bufo*), and *Heterelmis* (*H. glabra*, *H. obesa*, *H. obscura*, and *H. simplex*), occurring in all levels (except *H. simplex*, absent from R2 and R1 of levels 3 and 4, respectively). *Cylloepus atys* shares the same distribution pattern as *H. simplex*, while *Hexacylloepus metapa* and *Huleechius spinipes*, both occur in all altitudinal levels but are curiously absent from river 1 of level 4. *Macrelmis graniger* and *M. leonilae* are present in all rivers, while *Macrelmis* sp. is present only in river 2 of level 5. *Microcylloepus* (*M. inaequalis*, *M. troilus*, and *M.* sp.) are present in all altitudinal levels, however *M. troilus* is absent in river 1 of level 4 and river 1 of level 5. *Phanocerus clavicornis* has a fragmented distribution, occurring in levels 1, 3, and 4, while *Hexanchorus usitatus*, *Neoelmis apicalis*, and *Onychelmis longicollis* are present in all rivers from levels 1–3.

Dytiscidae (see some representatives on Fig. 4), the second most diverse family, is characteristic of the higher levels (i.e., levels 4 and 5), with all genera represented by only one species. *Copelatus distinctus*, present in all rivers of levels 3–5, has the largest vertical distribution. *Platambus americanus*, *Ilyobiosoma flohrianum*, *Laccophilus proximus*, and *Clarkhydrus* sp. are present in levels 3 and 4, however only *P. americanus* is present in all four rivers of these levels. *Bidessonotus championi*, *Liodessus affinis*, *Uvarus subornatus*, and *Neoclypeodytes fryii* are present in level 4, nevertheless only the latter species occurs in both sampled rivers. *Rhantus gutticollis* and *Thermonectus nigrofasciatus* are only present in river 2 of the highest level.

Dryopidae (see some representatives in Fig. 4) is present in the three lowest levels, with *Dryops mexicanus* and *Helichus suturalis* present in all rivers of such levels, while *Elmoparnus pandus* occurs only in level 1. *Epimetopus thermarum* (Epimetopidae),

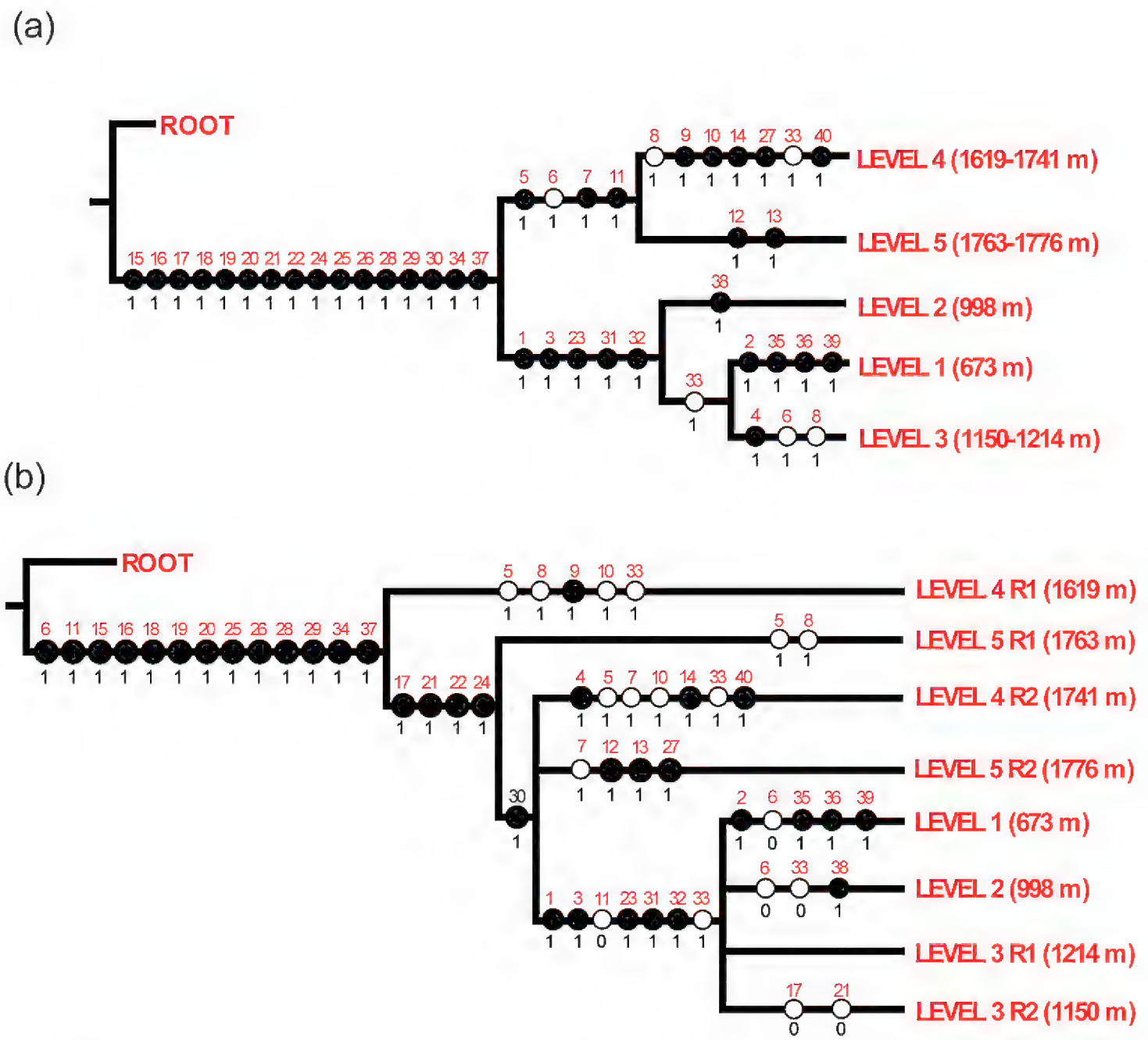

Figure 3. Parsimony Analysis of Endemicity (PAE) of the altitudinal levels and sites of the aquatic beetle fauna of Volcán Tacaná, Chiapas, Mexico **A** most parsimonious tree of the five sampling levels, with levels 3–5 considered each as a unit (number of steps = 43, consistency index (CI) = 93, retention index (RI) = 83) **B** strict consensus of the five most parsimonious trees of the five sampling levels, with levels 3–5 considered as two separate units each (number of steps = 53, consistency index (CI) = 75, retention index (RI) = 63). Red numbers = species (see Table 1); 1 = presence, 0 = absence, black circles = single event or first appearance, white circles = independent event or reversal (disappearance).

Gyretes boucardi (Gyrinidae), and *Lutrochus* sp. (Lutrochidae) occur only in level 1, while *Tropisternus fuscitarsis* (only recorded hydrophilid) is present in level 2, and *Notomicrus sharpi* (only noterid) occurs only in river 2 of level 4. Hydraenidae (*Hydraena* sp.) was present in all sampled rivers.

Biogeographical affinity of the aquatic beetle fauna

We attempt a general characterization of the fauna applying the criterion of Nearctic and Neotropical regions of Morrone (2006, 2017, 2019). Despite altitude of the

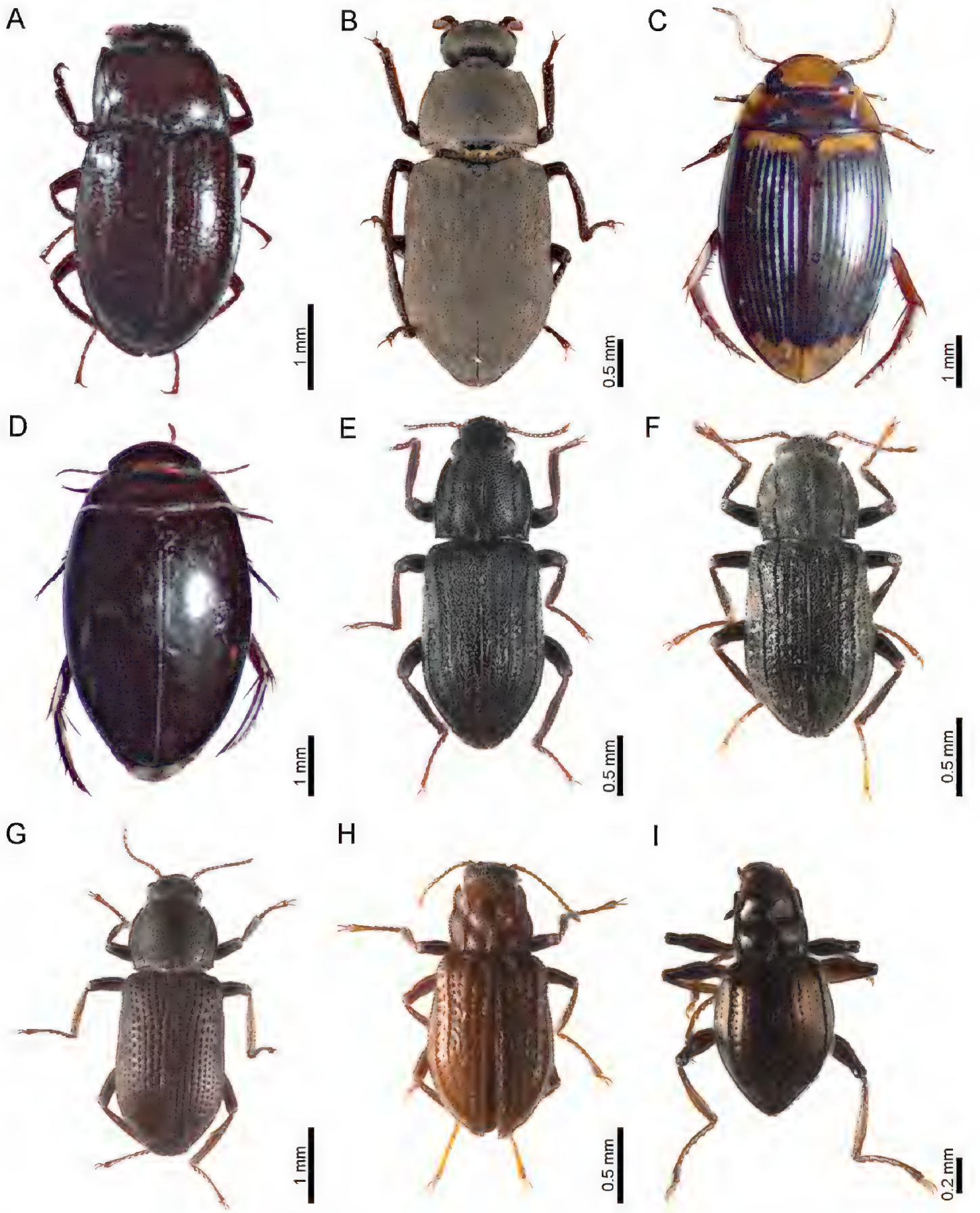

Figure 4. Habitus of representative species of the three most diverse aquatic beetle families from Volcán Tacaná, Chiapas, Mexico **A** *Elmoparnus pandus* Spangler & Perkins, 1977 (Dryopidae) **B** *Helichus suturalis* LeConte, 1852 (Dryopidae) **C** *Copelatus distinctus* Aubé, 1838 (Dytiscidae) **D** *Platambus americanus* (Aubé, 1838) (Dytiscidae) **E** *Cylloepus atys* Hinton, 1946 (Elmidae) **F** *Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020 (Elmidae) **G** *Macrelmis leonilae* Spangler & Santiago-Fragoso, 1986 (Elmidae) **H** *Microcylloepus Troilus* Hinton, 1940 (Elmidae) **I** *Onychelmis longicollis* (Sharp, 1882) (Elmidae).

sampled rivers, all species collected have distribution records within the Neotropical region (i.e., all levels present species of Neotropical affinity). About 60% of the species (24 out of 40) have a predominantly Neotropical distribution, while the remaining 40% (16 species) have a wide distribution in the New World, among which the elmids *Heterelmis glabra*, *H. obesa*, *H. obscura*, and *Huleechius spinipes* occur in all altitudinal levels (670–1,776 m); *Helichus suturalis* (Dryopidae), *Neoelmis apicalis* (Elmidae), and *Tropisternus fuscitarsis* (Hydrophilidae), *Epimetopus thermarum* (Epimetopidae) occur only in the two lowest levels (670 and 998 m); while *Notomicrus sharpi* (Noteridae) and the dytiscids *Laccophilus proximus*, *Liodessus affinis*, *Neoclypeodytes fryii*, *Rhantus gutticollis*, and *Thermonectus nigrofasciatus* occurr only in the two highest levels (1,610–1,776 m). Other two species with Neotropical and Neartic records have a fragmented vertical distribution (the elmid *Phanocerus clavicornis*) or occur in the three highest levels (the dytiscid *Copelatus distinctus*).

Among the 20 species of Elmidae, 14 occur only in the Neotropical region, while the remaining six, particularly those of *Heterelmis*, have a wide distribution (i.e., they occur in the Nearctic and Neotropical regions). Most dytiscid species, six out of 11, have a wide distribution through the Nearctic and Neotropics, while the other five occur only in the Neotropical region. Elmidae and Dysticidae have 80 and 50% of their distribution in the Brazilian subregions and the Mexican Transition Zone, respectively, with especial affinity to the Mesoamerican and Pacific domains. Dryopidae is represented by three species, two of them with records in the Neotropical region (Brazilian subregions and the Mexican Transition Zone) and one with Nearctic and Neotropical distribution. Gyrinidae (*Gyretes boucardi*), Hydraenidae (*Hydraena* sp.), and Lutrochidae (*Lutrochus* sp.), also have species with Neotropical affinity, whereas Epimotopidae (*Epimetopus thermarum*), Hydrophilidae (*Tropisternus fuscitarsis*), and Noteridae (*Notomicrus sharpi*) have species with a wide distribution in the New World. The latter six families also have an affinity to the Brazilian subregions, particularly to the Pacific and Mesoamerican domains.

Discussion

Aquatic beetles were present at the five sampling levels (L1, 673 m; L2, 998 m; L3, 1,150–1,214 m; L4, 1,619–1,741 m; and L5, 1,763–1,776m). This agrees with the widespread distribution of aquatic beetles, as well as their high capacity to inhabit different aquatic environments from sea level to mountains of 4,000 m high or more (Jäch and Balke 2008; White and Roughley 2008). Despite their broad presence in the volcano, aquatic beetle species were not distributed homogeneously along the altitudinal gradient, which is congruent with a high endemism in almost all families of this group, particularly those of lotic systems in warm climates (Jäch and Balke 2008).

Elmidae (riffle beetles) was the dominant group (20 spp.) and was present in all sampling levels. This coincides with previous findings in the Neotropics (e.g., Arias-Díaz et al. 2007; Huanachin-Quispe and Huamantico-Araujo 2018; Mosquera-Murillo and Sánchez-Vázquez 2018; Passos et al. 2018). General characteristics of the streams on a

volcanic bedrock with a variety of substrates, such as gravel, leaf litter, logs, and aquatic macrophytes, probably contributed to maintain a high diversity of elmids as reported by Elliot (2008) and Mosquera-Murillo and Sánchez-Vázquez (2018). Species of the New World genera *Heterelmis*, *Macrelmis*, and *Microcylloepus*, and of the Neotropical *Austrolimnius* were present at all levels, while the Neotropical *Hexanchorus*, *Neoelmis*, and *Onychelmis* were restricted to levels 1–3.

Dytiscidae (predaceous diving beetles) was the second most diverse group (11 spp.) and was present mostly at levels 4 and 5, with only one species (*Copelatus distinctus*) at levels 3–5. Three species, *Bidessonotus championi*, *Ilybiosoma flohrianum*, and *Uvarus subornatus* were only observed at L4 (R2, 1,619 m), while *Rhantus gutticollis* and *Thermonectus nigrofasciatus* appeared only at L5 (R2, 1,776 m). This distribution may relate to the size of the streams at the higher levels, which were generally smaller and with weaker currents, so pools were more common, which appeared to be a suitable habitat for dytiscids; most collecting of dytiscids was at depositional zones of the stream. This agrees with a general preference of this family for lentic systems (Miller and Bergsten 2016; Benetti et al. 2018).

Dryopidae was the third family in species richness (3 spp.) and was present at lower elevations, with *Dryops mexicanus* and *Helichus suturalis* at levels 1–3, and *Elmoparnus pandus* only at level 1. This is a mostly tropical family, which appears to explain their presence at low elevations, although there are records at higher elevation in other areas (Huanachin-Quispe and Huamantico-Araujo 2018). This family includes species that may be observed in both lotic and lentic environments, however, many of the species may be present near the water margin or even outside (Jäch and Balke 2008), also their larvae are terrestrial. This particular biology may indirectly restrict the presence of adult dryopids at such lower elevation sites. During collecting, specimens were only found submerged associated to substrates.

The rest of the families were represented by one species each. Hydraenidae (*Hydraena* sp.) was observed at the five sampling levels, which agrees with the broad distribution of the group and that species of this genus occupy different types of habitats, from small streams to large rivers (Trizzino et al. 2013). Noteridae (*Notomicrus sharpi*) was only present at level 4 (river 2, 1,619 m), which is above the previous known altitudinal record; as dytiscids, noterids prefer environments with slow current and some depth (Megna and Deler 2006), which includes the small pond (with macrophytes) at one side of the main stream where the only specimen was captured. Epimetopidae (*Epimetopus thermarum*), Gyrinidae (*Gyretes boucardi*), and Lutrochidae (*Lutrochus* sp.) were only recorded at level 1 (693 m). It is known that *Epimetopus* is attracted to lights (Perkins 2012), this agrees with our findings as specimens were captured with a bucket light trap. *G. boucardi* was collected in October, agreeing with White and Roughley's (2008) time of emergence of late summer and early fall for the species; specimens were captured in an adjacent pool forming a large aggregation, *Lutrochus* sp. was only found at level 1, with specimens captured on macrophytes; this group is typically from lotic systems; however, it has been little studied in Mexico. Finally, Hydrophilidae (*Tropisternus fuscitarsis*) was only recorded at level 2; it is interesting this representative family was only present with one species, which was collected with bucket light trap, probably indicating a not very suitable habitat for the group in a volcanic-based ecosystem.

Species observed in levels 1–3 are usually of Neotropical affinity, while in levels 4 and 5 species with both Nearctic and Neotropical distribution increase. In general, most of the species are of Neotropical distribution with an affinity for the Pacific and Mesoamerican domains, which coincides with Morrone and Márquez (2001), who observed that the Coleoptera fauna of the Chiapas Highland province is related to the Veracruzan and Pacific Lowlands provinces, which are part of the Mesoamerican domain. The relationship between the Chiapas Highland province and Veracruzan and Pacific Lowlands provinces was confirmed by Morrone (2019). This general partition in two groups of altitudinal levels, 1–3 and 4 + 5, is supported by a PAE analysis, pointing out to a preliminary general pattern of altitudinal distribution for the aquatic beetle fauna of Volcán Tacaná.

Conclusions

The aquatic beetle fauna of Volcán Tacaná presents a high diversity, with Elmidae, Dystiscidae, and Dryopidae as the most species-rich families, being responsible for 85% of the species. Some families (e.g., Hydraenidae and Elmidae) are distributed along all the altitudinal range, while Dytiscidae is present particularly at the higher altitudinal levels (1,619–1776 m); Noteridae is also present at high altitude, but only in a river located at 1,741 m. Remaining families, Dryopidae, Epimetopidae, Gyrinidae, Hydrophilidae, and Lutrochidae are present in lowlands (670–1,214 m). The aquatic beetle fauna of Volcán Tacaná presents a general partition in two well-defined groups: a lower altitude fauna (between 670, 934 and 1,150–1,214 m, levels 1–3) and a higher altitude fauna (between 1,619 and 1,776 m, levels 4 and 5). This fauna has an affinity to the Pacific and Mesoamerican biogeographic domains.

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Appendix 1

Table A1. Collecting data of examined material of the new records of species for Mexico; all specimens are deposited at Colección Nacional de Insectos (CNIN), UNAM. LV1-LV5 = sampled levels; R1 and R2 = sampled rivers; m = male, f = female; * = specimens collected with bucket light trap (as explained in materials and methods).

Sample data (day/month/year)	ELMIDAE				DYTISCIDAE
	Cylloepus atys Hinton, 1946	*Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020	*Hexanchorus usitatus* Spangler & Santiago-Fragoso, 1992	*Onychlemis longicollis* (Sharp, 1882)	*Bidessonotus championi* J. Balfour-Browne, 1947
10/02/2018	LV1R1 (2m)	LV1R1 (7m, 4f)			
11/02/2018	LV2R1 (1m)	LV2R1 (2f)			
13/02/2018				LV1R1 (1f)	
17/02/2018					LV4R2 (1m)
10/03/2018		LV1R1 (2m, 3f)	LV1R1 (10m, 8f); LV2R1 (1m, 2f)*		
09/04/2018			LV1R1 (10m, 14f)		
10/04/2018		LV2R1 (1m, 3f)			
11/04/2018				LV3R1 (1m); LV3R2 (2f)	
13/04/2018		LV3R2 (2m, 2f)			
20/04/2018	LV5R1 (1m, 1f)				
07/05/2018		LV1R1 (3m)	LV1R1 (44m, 58f); (59m, 76f)*		
09/05/2018	LV2R1 (1m, 1f)	LV2R1 (2m, 2f)			LV2R (1f)
11/05/2018	LV3R1 (1f)	LV3R1 (1m, 2f)			
12/05/2018		LV3R2 (2m, 1f)	LV3R2 (28m, 26f); (2f)*		
08/06/2018	LV1R1 (1f)	LV1R1 (2m, 6f)			
09/06/2018		LV2R1 (4m, 9f)			
15/06/2018	LV4R2 (1m, 3f)				
22/06/2018	LV5 R1 (1m)				
08/07/2018		LV1R1 (3m, 5f)	LV1R1 (34m, 38f); (16m, 63f)*		
09/07/2018	LV1R1 (3m, 7f)	LV2R1 (45m, 31f)	LV2R1 (10m, 18f); (15m, 11f)*		
10/07/2018		LV3R2 (12m, 25f)	LV3R2 (17m, 24f)		
11/07/2018		LV3R1 (6m, 3f)	LV3R1 (32m, 25f)		
13/07/2018		LV4R2 (1m)			
14/07/2018	LV4R1 (1m); LV4R2 (1m)	LV4R2 (1f)			
20/07/2018	LV5R1 (1f)	LV5R1 (2m, 3f)			
07/08/2018	LV1R1 (2m, 1f)	LV1R1 (10m, 19f)	LV1R1 (1m); (1m, 2f)*		
08/08/2018	LV2R1 (1f)	LV2R1 (27m, 20f)			
10/08/2018	LV3R1 (1m)	LV3R1 (8m, 13f); LV3R2 (20m, 43f)	LV3R1 (1m)		

Sample data (day/month/year)	ELMIDAE				DYTISCIDAE
	Cylloepus atys Hinton, 1946	*Hexacylloepus metapa* Silva-Polizei, Barclay & Bispo, 2020	*Hexanchorus usitatus* Spangler & Santiago-Fragoso, 1992	*Onychlemis longicollis* (Sharp, 1882)	*Bidessonotus championi* J. Balfour-Browne, 1947
12/08/2018	LV4R2 (3m, 4f); LV4R2 (3m, 4f)				
13/08/2018		LV4R2 (1f)			
17/08/2018	LV5R2 (6m, 2f)				
04/09/2018		LV1R1 (10m, 3f)	LV1R1 (34m, 17f)		
05/09/2018		LV2R1 (1m)			
07/09/2018		LV3R1 (4m, 2f)			
03/10/18		LV1R1 (2m, 2f)	LV1R1 (11m, 26f)		
04/10/18			LV2R1 (6m, 13f)		
12/10/2018	LVR2 (2f); LV5R2 (1m, 1f)				
02/11/2018			LV1R1 (5m, 6f); LV2R1 (10m, 5f)		
07/11/2018		LV3R2 (1m, 2f)	LV3R2 (4m, 8f)		
23/11/2018	LV5R2 (2m)	LV5R1 (1f)			
03/12/2018		LV2R1 (2m, 3f)	LV2R1 (3m, 7f)		
04/12/2018	LV4R2 (2f)				
06/12/2018			LV3R2 (3m, 13f)		
09/12/2018		LV5R1 (2m)			
04/01/2019	LV2R1 (2f)		LV2R1 (7m, 15f)		
06/01/2019		LV3R2 (1m, 2f)	LV3R1 (2m, 2f)		
04/02/2019	LV1R1 (4f)	LV2R1 (1m, 3f)	LV1R1 (1m, 7f); LV2R1 (6m, 10f)		
05/02/2019			LV3R1 (12m, 19f)		